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## THE ORIGIN OF THE SPOROPHYTE.

BRADLEY MOORE DAVIS.

ONE of the most interesting peculiarities of plant life is the striking alternation of generations characteristic of all groups above the algæ and fungi (thallophytes). It is customary to call these two generations by names that indicate the end of their life activities. The gametophyte is the sexual plant, developing the sexual cells or gametes. The sporophyte is asexual, producing spores. These functions of gametophyte and sporophyte have very few exceptions among the higher plants, the latter falling under the head of apospory and apogamy and resulting, at least, in part from abnormalities of environment. The fertilized egg always develops into a sporophyte and the asexual spore, on germination always produces the gametophyte.

The life history becomes then a rhythmical alternation of gametophyte and sporophyte only disturbed when a generation introduces organs for vegetative reproduction and thus makes possible a series of like individuals before the next generation. Such methods of vegetative reproduction by brood organs (gemmae), buds, bulbs or various fragments are not uncommon in the gametophytes of mosses and liverworts and are very common in the sporophyte generations of the seed bearing plants. Since it is vegetative reproduction and the offspring are literally chips from the parent block they in no way effect the underlying principles governing the alternation of generations.

These principles have become better understood with advances in our knowledge of cell structure in plants, and certain very interesting facts are now known which indicate that the peculiarities of gametophyte and sporophyte are due to structural conditions of the protoplasm that may in a measure be determined. So the problems have become largely an analysis of the events in the cell activities preceding the formation of sexual cells, also at fertilization, and immediately afterward with the development of the fertilized egg, and similarly the period of

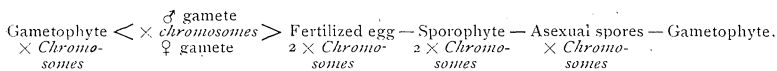
spore formation and germination of the asexual spore has been made the subject of careful study. It is evident that the critical periods of the plant's life, when the changes are the greatest, come with the passing of one generation over to the next or in other words at the periods of gametogenesis and sporogenesis with the early developments following each of these processes. We have now an accumulation of studies upon this subject from all three of the great groups of higher plants (bryophytes, pteridophytes, and spermatophytes) and in certain regions the investigations have been numerous. They have uniformly yielded the same results in certain particulars that have established a foundation for some very interesting speculations on the essential differences between the sporophyte and gametophyte.

It will be apparent that these differences must be very fundamental because they are the basis of extensive evolutionary processes with the universal tendency to separate the gametophyte and sporophyte further and further from one another in structure and life activities. From the conditions among the bryophytes in which the sporophyte is so closely associated with the gametophyte as to have been called its fruit by the early botanists, we pass through the pteridophytes to the spermatophytes where somewhat analogous conditions are found in which, however, the relations between the two generations are exactly reversed. Among the seed bearing plants the gametophyte has become so reduced as to live parasitically upon the sporophyte passing its life in the interior of the asexual generation which is thus made the phase that performs the vegetative activities that we expect of plant life. There is no more interesting province of plant morphology than that which traces the evolution of the sporophyte and degeneration of the gametophyte as one passes from the liverworts to the higher plants. There are involved in these processes a number of evolutionary principles of the greatest significance but they do not fall within the range of the present paper.

Can we establish a physical basis for the differences between sporophyte and gametophyte in the cell and nuclear activities during the life history. This has been attempted chiefly through the study of the number of chromosomes present in the nucleus

at the critical periods when one generation passes into the other. The results have been remarkable. The nucleus of the gametophyte generally presents a fixed number of chromosomes as shown in the figures of nuclear division in the various tissues. We may let  $x$  stand for this number, which is generally not very large (*e. g.*, 4 in *Anthoceros*, 8 in *Pellia*, 12 in *Osmunda*, 12 in the lily, etc.) The nuclei in the sexual cells (gametes) have this gametophyte number ( $x$ ). Their fusion, during the sexual act, gives a sexually formed spore whose nucleus has  $2x$  chromosomes, double the number of the gametophyte. This double number ( $2x$ ) prevails through the entire sporophyte generation up to the time when the sporogenous tissue (archesporium) appears. The events of sporogenesis reduce the number by one half bringing the asexual spore back to the condition of the gametophyte with  $x$  chromosomes.

This cycle by which the number of chromosomes is doubled and then reduced probably holds true for all plants above the thallophytes, the conclusions being based upon the study of several liverworts and pteridophytes and a larger number of spermatophytes. The essential facts of the history may be expressed in an abbreviated form as follows.



Reduction of the chromosomes is a phenomenon that has been much studied in connection with sexual processes, especially among animals. It is believed to result from the supposed necessity of keeping the chromosomes in all organisms relatively fixed in number. Since the number of chromosomes is doubled with every nuclear fusion in the sexual act the amount of chromatin would increase indefinitely and in geometrical progression were there not a device for diminishing the quantity at some time in the life history.

If the question is asked why are the chromosomes so important and why should their number be so significant, no answer can be very satisfactory for our deep ignorance of the function of the nucleus is exposed. However, the more detailed the studies upon the structure and activities of the cell the greater

has become the conviction that the chromosomes carry the keys to many and probably the most important problems of development and heredity. We do not know what the chromosome does but its characteristic activities during nuclear division and its behavior at critical periods in the life history are so remarkable that the assumption of its importance in these events is quite justified. The most attractive theory of reduction phenomena assumes that specific characters are largely defined by the amount and nature of the chromatin in the nucleus and that a species, to keep true, must so provide that the chromatin content is relatively stable from generation to generation.

Reduction of the chromosomes at some period of the life history is almost universal among higher animals and plants but we should note an important difference between the two groups in the manner in which this is accomplished. Briefly stated for animals, the reduction occurs just before the formation of the sexual cells (gametes) which have in consequence one half the number of chromosomes characteristic of the organism. The fertilization of the animal egg by the sperm brings the male and female nuclei together and as a result of their fusion the number of chromosomes becomes again normal.

In plants above the thallophytes the history is very different and in sharp contrast to that of the animal. There is no reduction at the time when the gametes are formed. The gametes have consequently the same number of chromosomes as the sexual plant (gametophyte). Their fusion gives to the sexually formed spore double the number characteristic of the gametophyte. This fact is believed to be largely responsible for the peculiarities of the asexual generation that follows. The sporophyte runs through its vegetative development, without any change in the double number of chromosomes, to the time of spore formation when the sporogenous tissue (archesporium) is differentiated. There is then a period of growth during which some or all of the archesporial cells become spore-mother-cells. And during that preparation for spore formation (sporogenesis) the number of chromosomes is reduced by half, becoming again the number of the gametophyte. The reduced number first appears in the nuclear divisions inside of the spore-mother-cell

preparatory to the formation there of the characteristic group of four spores.

It will thus be seen that there can be no genetic relationship between the reduction phenomena of higher plants and animals. They are not found at the same points in the life history and there are also fundamental differences in the details of the process that cannot be considered here.

With these points understood the sporophyte generation takes on new interest in relation to sexual processes in plants for it appears to be a development peculiar to this group of organisms and probably related to a form of sexuality that differs from that of animals in important respects. These differences concern the maturation of the gametes which in animals takes place with a very characteristic process of chromosome reduction and in plants without this phenomenon.

So little is known about the origin of sex in animals that satisfactory comparison with the much better understood history for plants, is not possible. We have already discussed that topic<sup>1</sup> and also sexual evolution.<sup>2</sup>

As there is no reduction phenomena in plants at the time when sexual cells are formed perhaps we find in this fact a clue to the reason of the sporophyte generation and its origin. It must be clear that the most promising line of investigation would deal with the doubling of the chromosomes at the sexual act and the later reduction to the gametophyte number at the end of the sporophyte generation.

The final explanation of the problems can only come through the study of plants below the Bryophytes, that is among the Thallophytes, and we have had as yet very little detailed research on this point. So this paper must deal largely with speculations. We know positively the main facts of sexual processes and chromosome reduction in groups above the Thallophytes but for this group almost nothing.

Nevertheless, we are justified in considering an hypothesis of

<sup>1</sup> Davis, The Origin of Sex in Plants. *Popular Science Monthly*, Nov. 1901, p. 66.

<sup>2</sup> Davis, The Evolution of the Sex in Plants. *Popular Science Monthly*. Feb. 1903, p. 300.

the origin of the sporophyte and its relation to reduction phenomena and this hypothesis may be tested among the thallophytes and must stand this test if the suggestions are to become a theory.

An explanation of the sporophyte upon a physical basis must consider the problem in terms of protoplasmic organization. It must attempt to isolate the structures and qualities given to the egg by fertilization. It must determine the potentialities of the sporophyte generation and also explain why this structure should finally produce spores whose protoplasm returns to the condition of the gametophyte.

The sexual act in all plants above the thallophytes doubles the number of chromosomes. This is the only morphological change that we can observe in the structure of the protoplasm. It is scarcely probable, however, that the doubling of the chromosomes introduces all of the changes that come over the fertilized egg when it takes on the qualities that compel its development into a sporophyte. There is of course the mingling of many substances when the sperm fuses with the egg and we have good reasons to believe that all regions of the protoplasm are effected. But the nucleus gives us the most marked evidence of change in structure and this is shown conspicuously in the number of chromosomes. That the potentialities of the sporophyte are chiefly bound up in the protoplasmic structure of the egg, there can be little doubt. Fertilized eggs of plants above thallophytes cannot be made to develop gametophytes. They are wound up, to use a homely expression, to produce sporophytes and this they will always do under normal conditions. Some peculiar forms that omit certain stages in the alternation of generations are believed to be the products of unusual environmental relations. They are apogamous or aposporous or examples of regeneration and are the exceptions that prove the rule.

The potentialities of the sporophyte generally remain indefinitely long in all regions of the plant where the tissue is embryonic in character, *i. e.*, at all growing points or meristematic areas. These tissues will reproduce the sporophyte or add to its growth as long as they live and retain their undifferentiated character.

But more specialized and older parts of the plant show other characteristics. Some of these regions become specialized for various vegetative activities, assimilation, conduction of water, storage, etc.; some become protective, as the epidermis and cortical regions, and some strengthening. There comes however sooner or later to certain of these older portions another activity, that of spore formation or sporogenesis.

Sporogenesis in the simpler sporophytes generally involves extensive regions of the plant, sometimes almost the entire structure as in certain liverworts (*Ricciales*). However the evolutionary tendency among higher forms is to develop more extensively the purely vegetative tissues thereby reducing proportionately the spore bearing areas. This very important principle involves the sterilization of sporogenous tissue and may be traced in a very interesting manner as the sporophyte increases in complexity until the sporogenous tissue becomes confined to special organs, termed sporangia. But we cannot consider this topic at the present time.

The significant result for us is the fact that at some period in the history of every sporophyte certain tissues return to the potentialities of the gametophyte and reproductive cells are formed which can only grow into gametophytes. The mechanism, wound up by the act of fertilization, runs down in a figurative sense and the protoplasm, losing its sporophyte characters, returns to the dead level of its ancestral plasm from the gametophyte.

The only evidence of this reversion to gametophyte conditions, as shown by the structure of the protoplasm, is in the reduction of the chromosomes. This occurs just before the sporogenous tissue (archesporium) is ready to form spores. The young cells of the archesporium emerge from their last vegetative division with the sporophyte number of chromosomes in their nuclei. There is then a period of enlargement during which some or all of the cells are stored with a rich supply of protoplasm becoming spore mother cells. During this period of enlargement the reduction phenomena takes place probably by the fusion of the chromosomes in the resting nucleus. The resting nucleus at this period is for some time in the state called synapsis when



the chromatin network is very much contracted, a very conspicuous condition which is not well understood. The first nuclear division in the spore mother cell presents the gametophyte number of chromosomes and this is followed by a second division so that four nuclei result, each of which is destined to preside over a spore.

The fact that the number of spores formed in each mother cell is four appears to have no important morphological significance. It has no connection with reduction phenomena which, as explained above, take place before these divisions. Among the seed plants this division is very frequently omitted in the megaspore mother cells which give rise directly to the gametophyte (embryo sac) thus cutting out a portion of the usual history in the development of spores.

However the fact that four spores are formed in each spore mother cell is interesting because almost universal among the bryophytes and pteridophytes and characteristic of pollen formation in the Spermatophytes. We can see no reason why the number should be four nor is any light thrown upon the problem from our knowledge of the thallophytes.

To summarize this explanation of the sporophyte; we assume that the fusion of gametes (fertilization) gives to the sexually formed spore a different mechanism from the parent gametophyte and this mechanism, under normal conditions, runs a course, producing the sporophyte. The result is a differentiation of the cells through a constant tendency to develop vegetative regions (somatic) in contrast to the reproductive tissue which is proportionally reduced in quantity. The latter (archesporium) generally appears at certain periods of development and in definite regions and represents the return of the sporophytic plasm to the potentialities of the gametophyte. We do not mean to imply that the entire development of the sporophyte is regulated from within, which conception would be ultra preformation. There must be numerous external factors (epigenetic) influencing the vegetative regions and affecting the organography of the plant and certainly the periods of spore formation. But there seems to be the best of evidence that the initial stimulus to sporophyte development comes from within. These are topics that may be

better discussed in a consideration of the evolution of the sporophyte than under the title of the present paper.

The origin of the sporophyte involves the examination of conditions previous to the bryophytes, *i. e.*, among the groups of the algæ and fungi (thallophytes) and we will now consider these.

As is well known the algæ and fungi present organisms far more various in the succession of forms comprising their life histories than the higher plants. There is no general rule of development in this assemblage of diverse groups but rather a number of habits presented by the divergent lines in relation to their various modes of life. In this respect the thallophytes stand in sharp contrast to all plants above the bryophytes. The antithesis of sporophyte and gametophyte, if present at all, is greatly obscured by the intercalation of many and various means of asexual reproduction which may give an indefinite and very irregular succession of individuals. For many years botanists have attempted to define among these lower plants life histories comparable to the alternation of gametophyte and sporophyte. Some of these suggestions appear probable, others have been completely disproved by experimental studies on development.

The test of an alternation of generation involving a gametophyte and sporophyte must always lie with the activities of the sexually formed spore. If this cell invariably produces a phase different from its parent plant then we may properly inquire whether such a structure does not have in itself potentialities that separate it as a distinctly new form of development. It may then be called a sporophyte in contrast to the gamete bearing individual and the succession of generations will be *antithetic* at this point in the life history.

It does not matter how numerous are the successions of generations which depend on various methods of asexual reproduction. They may occur directly before or after the sexual act or over a long intermediate period. Such generations are called *homologous* since they all produce the same form of plant. They do not affect the contrast of gametophyte and sporophyte whenever that change occurs in a life history.

The establishment of alternation of generations among the algæ and fungi depends on the determination of the various

phases as either *homologous* or *antithetic*. They are *homologous* when they can be made to develop indefinitely the same form of the plant successively, *antithetic* when the sexually formed spore always gives rise to a distinctly new phase. This test of the conditions in the life histories of the thallophytes is being generally applied throughout the group as opportunities are presented and has led to some interesting results.

Some forms, that at one time were thought to present tendencies towards an alternation of generation, are now known to give merely a succession of homologous phases. The zygospore of the moulds (Mucorales) and the eggs of *Vaucheria*, the Saprolegniales and probably the Volvocaceæ may on germination produce a series of asexual generations or they may pass at once back to the sexual plant according to the environmental conditions. So there can be no antithesis of sporophyte and gametophyte among these types. These facts have been thoroughly established experimentally by Klebs and illustrate clearly the method by which the problems are attacked. However, the details of the environmental conditions under which such plants become sexual or asexual cannot be given here.

Again, certain thallophytes whose sexuality is highly developed present life histories with but one phase, a sexual plant, and without the least tendency towards the development of a sporophyte generation. Notable examples are found in the Characeæ and Fucaceæ where the eggs on germination produce a sexual plant like the parent. The fact that the oospore of *Chara* develops a small filamentous structure preliminary to the establishment of the characteristic later growth does not affect the general principle. Investigations on the nuclear history of *Fucus* report a chromosome reduction after a peculiar manner that cannot be reconciled with the conditions known for groups above the bryophytes. The number of chromosomes is reduced one half just before the differentiation of the oogonium so that the gametes have half the number of chromosomes characteristic of the parent plant. After fertilization the egg has again the regular number and naturally develops into a plant like the parent. The life history may be outlined in this manner.

$$\begin{array}{c} \text{Sexual plant} < \frac{1}{2} \times \begin{array}{c} \text{♂ gametes} \\ \text{chromosomes} \end{array} > \text{Fertilized egg} - \text{Sexual plant.} \\ \times \text{chromosomes} & \quad \times \text{chromosomes} \end{array}$$

A comparison of this formula with that given at the beginning of this paper for all plants above the Thallophytes will make the peculiarities of *Fucus* clear. The reduction phenomena comes at the same period as in animals, *i. e.*, previous to the formation of the sexual cells, and the fertilization of the egg brings that structure back to the potentialities of the sexual plant. In contrast to *Fucus*, the conditions among the Characeæ appear to be very different. Investigations here have failed to establish a reduction of the chromosomes at the time the gametes are developed. We do not as yet know where the process occurs in this group.

These conditions in *Fucus* are unexpected and cannot be easily brought into sympathy with the processes of gametogenesis as illustrated in the higher plants. It is the only form among the thallophytes in which the count of the chromosomes has been made for the life history, and until we know the conditions in some of the other types it must remain a puzzle. We are quite in the dark as to its significance in the general problem of sexual evolution among plants and in its relation to alternation of generations. It may present an exception to the usual history of chromosome reduction among Thallophytes and this is to be hoped as otherwise further studies may greatly complicate the problems and require a reconsideration of the theories of the evolution of sex in plants and the origin of the sporophyte.

There are left several groups of thallophytes which are generally supposed to present phases in their life history that are either true sporophytes or indicate tendencies in that direction. The most pronounced evidences of a sporophyte generation are furnished by the red algæ (*Rhodophyceæ*), *Coleochæte* and the *Ascomycetes*. Tendencies in the direction of such alternation of generations are probably shown in *Edogonium*, *Sphaeroplea*, *Ulothrix* and the *Conjugales*.

The sexual reproduction of the red algæ presents peculiarities that have puzzled investigators for many years. The female gamete (carpogonium), after fertilization, gives rise to a more or less complex system of filaments that always remain attached to the parent sexual plant and in many forms are undoubtedly dependent upon it in part for nourishment and protection. Portions of these filaments and sometimes almost the entire struc-

ture become spores which on germination develop the sexual plant. In 1898 Oltmanns presented the suggestion that the filamentous growth from the female gamete was a true sporophyte. Although we lack the confirmation required by the close study of the details of nuclear activities, nevertheless the theory is very satisfactory especially in its explanation of certain peculiarities of this interesting process of development.

The simplest sporophytes among the red algæ are illustrated

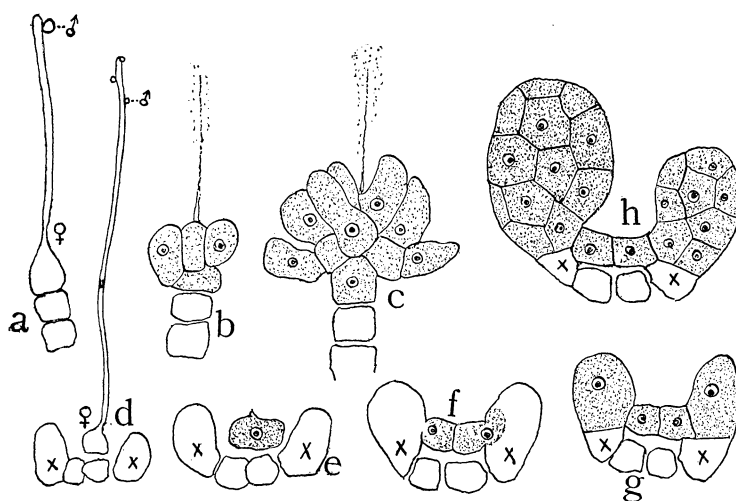


FIG. 1. Semi diagrammatic illustrations of supposed sporophyte of the Rhodophyceæ; shaded structures sporophytic; (x) auxiliary cells; a, b, c, Nemaion; d, e, f, g, h, Callithamnion.

by such forms as Nemaion (See Fig. 1, a, b, c) and Batrachospermum. Here we have a cluster of short filaments many or most of whose cells become spores. But among the higher red algæ the conditions are greatly complicated by certain cell fusions between the sporophytic growth and the filaments of the sexual plant (gametophytic). Certain cells of the gametophyte are set apart as large richly nourished auxiliary cells whose functions are to assist the developing sporophyte. The fusion of the sporophytic filaments with the auxiliary cells stimulates the growth of the former. It was at one time supposed to be sexual in character but is now believed to be for nutritive purposes alone. Apparently there are no nuclear fusions in these unions of cells but only the mixing of cytoplasm with its

opportunity for the extensive transfer of food material. The main points in this interesting process are illustrated for *Callithamnion* in Fig. 1, *d*, *c*, *f*, *g*, *h*.

The sporophyte of the red algæ holds a relation to the gametophyte somewhat similar to that in the bryophytes in as much as it is always attached to the latter generation. The sporophytic growth accompanied by developments, usually protective, on the part of the gametophyte constitutes the so-called cystocarpic fruit of the Rhodophyceæ. It should be noted, however, that this sporophyte does not exhibit the upward evolutionary tendencies towards independence so characteristic of the higher plants but rather a degree of dependence approaching parasitism.

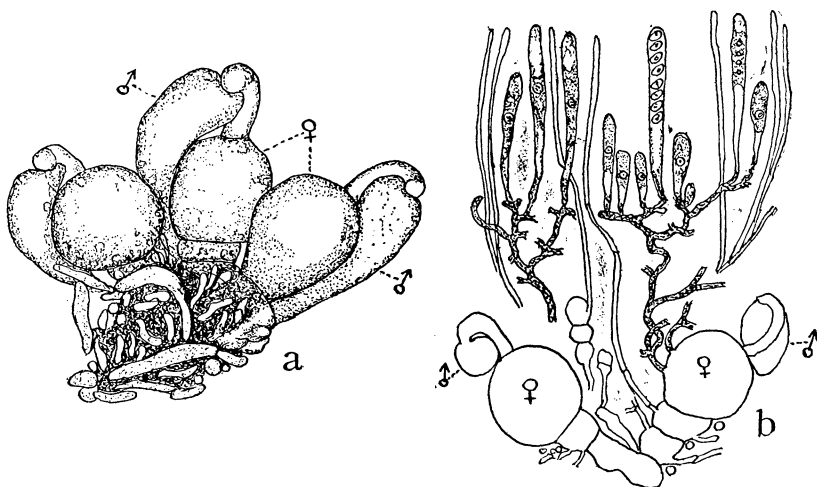


FIG. 2. *Pyronema*: a, Group of gametes; b, diagram of ascogenous hyphæ (shaded) in relation to the gametes and sterile mycelium of the sexual plant. (Somewhat modified after Harper).

The Ascomycetes furnish conditions somewhat similar to the Rhodophyceæ but here also we lack precise knowledge of nuclear structure at important periods of development. The female gamete, called here the ascogonium or archicarp, develops a system of filaments (ascogenous hyphæ) so closely associated with the parent organism that they can only be distinguished through special staining processes.

The ascogenous hyphæ develop asci, a form of sporangium

peculiar to the Ascomycetes, which are generally associated together and surrounded by an envelope thus constituting a fruit called the ascocarp. These conditions are illustrated somewhat diagrammatically in Fig. 2 for *Pyronema*, the form perhaps most completely studied.

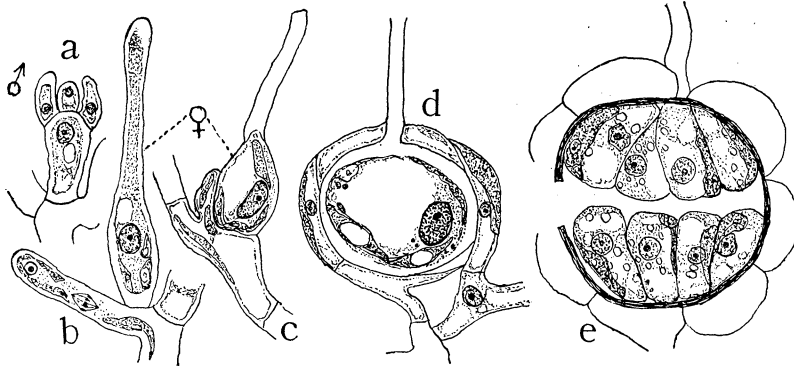


FIG. 3. Coleochaete: *a*, Group of antheridia; *b*, oogonium; *c*, fertilized egg; *d*, oöspore in cellular envelope; *e*, germinating oöspore showing tissue in its interior (sporophytic). (After Oltmanns.)

Coleochaete is a type upon which those who believe in a sporophytic generation among the thallophytes lay great stress. The principal reason for this emphasis is a certain resemblance in form between a cellular body developed by the fertilized egg and the simple sporophytes of the lower bryophytes. As is shown in Fig. 3, *d* and *e*, the fertilized egg after a period of rest develops in its interior a tissue each of whose cells gives rise to a zoöspore which on germination produces a sexual plant. This structure is very suggestive of the sporophyte of the simplest liverworts (*Ricciales*), but we know nothing about the chromosome history during its development. It is not safe to relate the liverworts to Coleochaete because the sexual organs are so different, for the archegonium is an organ that can hardly be derived from so simple a structure as the unicellular oogonium. However we can readily conceive the Coleochaetaceæ as a group tending to develop a sporophyte generation along somewhat parallel but totally independent lines from the Bryophytes.

Coleochaete is generally cited as the Thallophyte in which a sporophyte generation is most evident but in reality the develop-

ments from the female gametes in the red algæ and the Ascomycetes are far more elaborate and show a much higher grade of structural evolution. But the fact that the apparent sporophytic tendencies in these latter groups are long divergent lines related to the peculiarities of their modes of life and so very unlike that of the bryophytes has not given them the degree of attention in relation to the general problem that they deserve. If future studies upon their nuclear conditions support the theory of their sporophytic nature these structures should be cited as the highest forms of sporophyte among the thallophytes but of course in groups very far removed from the main line of ascent to the bryophytes.

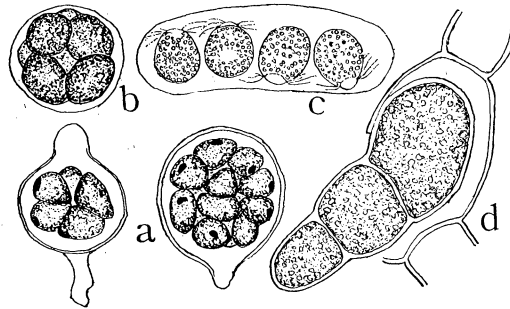


FIG. 4. Germination of the sexually formed spores of *a*, *Ulothrix*; *b*, *Sphaeroplea*; *c*, *d*, *Oedogonium*. (*a*, after Dodel-Port; *b*, Cohn; *c*, Pringsheim; *d*, Jurany.)

There are left several algæ somewhat similar to one another in the behavior of their oöspores on germination, and the peculiar group of the Conjugales. The fertilized eggs of *Ulothrix*, *Sphaeroplea* and *Oedogonium* (see Fig. 4) generally give rise to several zoöspores which develop into filaments like the parent plant. There is thus a short period after the stimulus of the sexual act when the protoplasm of the organism behaves differently from its usual vegetative activities. Some botanists consider this behavior the beginning of a sporophyte generation introduced after and the direct result of the sexual act. The union of gametes is supposed to give a product (the sexually formed spore) whose protoplasm has potentialities different from the parent plant. There is in general a greater vigor and prob-



ably a modified structure which demands some other form of expression than the vegetative activities characteristic of the species. Such a phase, intercalated after a sexual act, would start its peculiar period of activity because the protoplasm had a different chemical and physical composition from that of the parent plant. Its fundamental characteristics are therefore performed through the fusion of the gametes.

This view of the origin of the sporophyte as primarily the result of sexuality carries with it a comprehensive definition of the phase. It becomes a generation, always intercalated after the sexual plant, which is called a gametophyte by way of distinction. It is a generation always *antithetic* with the gametophyte because of potentialities within itself. When once thoroughly established, the sporophytic generation would be expected to have the power of developing the gametophyte only after it had passed through its characteristic history. The sporophyte could never be an *homologous* generation with the gametophyte in the way that succeeding generations of Thallophytes by asexual methods of reproduction are homologous with one another.

We should not expect the sporophyte to have arisen with the potentialities of immediate and extensive growth developments but rather as a small beginning such as may well be illustrated in *Ulothrix*, *Sphaeroplea* and *Oedogonium*. Here the peculiarities of the sexually formed spore seem scarcely more than an increased vigor that expresses itself in the formation of a number of reproductive cells. However, we know nothing of the nuclear activities in these forms and the assumption that the protoplasm of the sexually formed spore is structurally different from that of the gametophyte is speculation but seemingly reasonable. As has been stated, there are several thallophytes whose sexually formed spores develop directly into the sexual plant and indeed the egg of *Oedogonium* has been known to grow directly into a filament (Fig. 4 *d*). These forms must also be studied in comparison with the types in which the sporophyte generation seems well established.

The Conjugales present some interesting conditions. The union of the gametes gives a zygospore (see Fig. 5 *a*) that finally

contains a single nucleus although the fusion of the gamete nuclei is sometimes greatly delayed. The fusion nucleus divides into four nuclei previous to the germination of the spore but some of these degenerate. Thus in *Spirogyra* three nuclei break down so that only one is left at the time when the new filament ruptures the spore wall. In certain desmids (see Fig. 5) two of the original four nuclei degenerate and the remaining two enter into the formation of the pair of new desmids developed in each zygospore. It may be suggested that the division of the fusion nucleus apparently wasteful of material represents the expenditure of energy infused by the sexual act and consequently a sporophyte activity which is necessary to bring the protoplasm

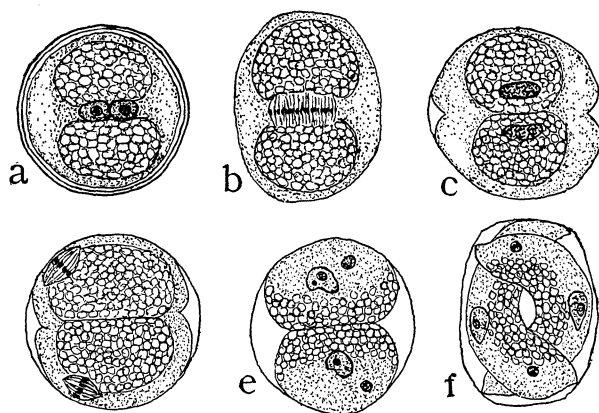


FIG. 5. Germination of the zygospore of a desmid (*Closterium*). (After Klebahn.)

back to the potentialities of the parent organism. But again we do not know the structural changes that take place in the nucleus of the Conjugales at and after the time of fertilization. Certain diatoms present activities resembling in some respects the Conjugales but the conditions are too complicated to be given here.

This attitude towards the significance of the nuclear divisions following the sexual act is the keystone to the theory of the *antithetic* origin of the sporophyte and its significance, a view held by many prominent botanists including Bower, Strasburger, and Klebs. The sexual act is assumed to give to the fused gametes an organization that will always tend to differ from that

of the parent plant. When the modification is sufficiently great we should expect a new or modified morphology in the resulting generation which would naturally react in a different manner to its environment. The new generation becomes then a phase intercalated after the sexual act and antithetic with the sexual plant (gametophyte).

In its earliest beginnings the sporophyte might differ so slightly from the gametophyte in its potentialities for development as to give no very decided results. Such expressions would be an indefinite cellular body such as is illustrated by *Coleochaete* or perhaps nothing more than a stimulus to develop several reproductive cells as may be observed in *Ulothrix*, *Ædogonium* and *Sphæroplea*.

An extensive elaboration of the sporophyte generation must follow from any changes that lead to complexity either of external conditions or internal structure through the mixing of protoplasm in the sexual act. The character of the evolution must depend largely upon the environmental relations, so that sporophytes should be expected to diverge in structure from their first inceptions. The most elaborate sporophytic developments in the algæ (*c. g.*, probably the *Rhodophyceæ*) cannot be like those of land plants, and those of fungi must be expected to present peculiarities of their own (*Ascomycetes*).

In closing we may summarize the principles that we have discussed in relation to the sporophyte.

First: Its origin, a phase intercalated after the sexual act because the fusion of gametes gives a protoplasm structurally different from that of the sexual plant (gametophyte).

Second: Its establishment as an *antithetic* generation through these peculiarities of protoplasmic structure that tend to express themselves in morphological developments different from the gametophyte, which developments are at all time influenced by environmental relations.

Third: Its end, the production of asexual spores with the potentialities of the gametophyte through a structural change in the protoplasm by which the sporophytic characters disappear and the ancestral qualities of the gametophyte again assert themselves.

The sporophyte will vary in complexity with the environmental conditions and the tendency must be always towards structural divergence. There are several well defined and very important principles responsible for these complexities and they will be considered in future papers dealing with the evolution of the sporophyte.

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